Effect of isolation on pairing success within an endangered population of Ortolan bunting (*Emberiza hortulana*) in Norway.

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FORORD

Først av alt vil jeg takke min veileder Svein Dale for stødig og god veiledning, entusiasme og hjelp – både under feltarbeid og i tiden etterpå for å få skrevet oppgaven ferdig. I tillegg må jeg takke Vegard Bunes og Christine Sunding for hyggelig selskap under feltarbeidet.

Mest av alt vil jeg takke deg Øyvind – for alltid å ha støttet meg, hatt troen på meg – det har betydd uendelig mye for meg. Tror ikke jeg hadde klart dette uten deg gutten min. Takk til mamma og pappa for å ha utvist den tålmodigheten bare foreldre kan ha og den støtten dere har gitt meg.

Takk til alle mine venner fra studietiden på Blindern som gjorde livet på lesesalen til en herlig og uforglemmelig tid.

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ABSTRACT

Small, isolated and fragmented bird populations are more vulnerable to extinction and studies have shown that they can have a high proportion of unpaired males. Female-biased natal dispersal could be an explanation of the low male pairing success. Indirect evidence has shown that such an effect operates between populations with different degree of isolation. How isolation affects male pairing success within a population is not well known, and in this study I examined isolation within the population of the endangered ortolan bunting (*Emberiza hortulana),* both between patches and between males in relation to pairing success. The aim was to test the hypothesis presented by Dale, that pairing success within small and fragmented populations may also be affected by degree of isolation. The ortolan bunting population has a skewed male-biased sex ratio, with a high number of unpaired males. Other factors that could have an effect on pairing success, like habitat and territory quality, patch size and patch population size were also examined. I found no effect of isolation on male pairing success within the population, neither on a territorial level nor on patch level. Patch size and patch population size did not have an effect on male pairing success, but habitat in territory showed a highly negative effect on pairing success within the habitat category recently cleared ground. I found no effect of isolation when including habitat in the main analysis. Even though Dales hypothesis was not confirmed in this study, there is indirect evidence from the last years research on the species, that it could operate on a larger scale within the population.

1 INTRODUCTION

1.1 Human impact on habitats

Humans have an enormous influence on earth, its ecosystems and its animal populations, and it is our activities that are the primary cause of most species declines. We have altered between one-third and one-half of the earth's surface (Vitousek et. al. 1997) and it should be no surprise that for instance in globally threatened birds, 99 % of these are at risk because of human activities such as agriculture, logging, hunting and trapping (BirdLife International 2000). With habitat destruction comes usually habitat fragmentation which could lead to extinction in many populations, isolation of remaining populations and those populations remaining may face new threats (Holsinger 2000). It is of invaluable importance to understand the causes that can increase the threat of extinction in order to make proper management plans and save the specific species.

1.2 Small, isolated and fragmented populations

Populations which are small, isolated and fragmented are more vulnerable to extinction through stochastic perturbation like loss of genetic variation, demographic stochasticity (i.e. random variation in sex ratio, mortality or reproduction) and environmental stochasticity (i.e. in abiotic (weather, natural catastrophes) and biotic (habitat, predators, competitors, disease) factors) (Shaffer 1981, Beissinger & McCullough 2002). There must also be a balance between immigration and emigration for the population to persist (Hanski 1999), and isolated populations are unlikely to persist unless their annual growth rates are high relative to the variability in growth rate (Holsinger 2000). A high growth rate in a population is dependent of high recruitment and therefore an equal amount of males and females contributing to reproduction. A skewed sex-ratio would lead to a high proportion of unpaired individuals which again would influence on the reproductive output and the population would decrease. In small and isolated populations this would be the first sign that the population are heading towards extinction (Dale 2001b). The population would also be much more vulnerable to stochastic events. Knowledge of pairing success in small and isolated populations is therefore important to understand the viability of the population.

In several studies a high proportion of unpaired males have been found in small, isolated and fragmented populations (reviewed by Dale 2001b, Zanette 2001, Steifetten & Dale 2006). Dale (2001b) argues that this could be indirect evidence that locating a mate between populations with different degrees of isolation within the species' distributional

range could be difficult. In bird populations the male are often the philopatric sex while the female have a greater natal dispersal (Greenwood 1980). Dale (2001b) argued that this female-biased natal dispersal would make a fragmented and isolated population more vulnerable to decline and head towards extinction, especially in a migratory species. Females have a limited capacity to search for unpaired males (Dale et. al. 1992, Dale & Slagsvold 1996) and females may become lost from the breeding pool (Dale 2001b). In fragmented and isolated populations females will have a greater risk of dispersal to unsuitable habitat than to small suitable habitat patches. Thus, the population could experience a net emigration of females because of the female-biased natal dispersal (Dale 2001a, 2001b). Together with the lack of female dispersal between fragments (Cooper & Walters 2002) this will lead to a high proportion of unpaired males within the population.

Since females also have a limited time to find a mate (Dale et. al. 1992) and that it could be costly (Slagsvold et. al. 1988) makes it probable that the more fragmented and isolated the patch within the population are the less likely it is that the female will be visiting. There should also be a higher probability of locating a mate in large and continuous populations, than in the centre of small or fragmented populations (Dale 2001b, Wells et. al. 1998). How isolation and patch size affect pairing success within a population is not well known. Isolation between patches and between individuals or how patch size would influence on pairing success should be devoted some more study, because pairing success is a vital demographic parameter. This could contribute to understanding more about the underlying causes of declines in small, fragmented and isolated populations.

The Norwegian population of ortolan bunting lies highly isolated in the northernmost periphery of the species distribution range in Europe and with a distance of 250 km (Steifetten 2006) to the nearest Swedish population of the species. Also the population is fragmented in local population patches of different sizes within a distribution range of about 500 km^2. The population shows a strongly skewed sex-ratio, with an excess of unpaired males. For years the population of ortolan bunting in Norway has showed a highly declining tendency and there has been a tendency that local populations far from the main area (central parts of Hedmark county) have become extinct.

In this study I examine isolation within the population, both between patches and between males in relation to pairing success. Other factors could have an effect on pairing success, like habitat and territory quality (Burke & Nol 1998), patch size and patch population size (Dale 2001b). Females usually locate a male by its song (Eriksson & Wallin 1986) and therefore it should be a higher chance for a female to detect patches with many singing males

than those with only a few males. To elucidate possible effects of these factors on pairing success, I also tested for habitat choice, patch size and patch population size.

The data were analysed with the aim of testing the hypothesis presented by Dale (2001b) (outlined above) that pairing success within small and fragmented populations may also be affected by degree of isolation. I have drawn some specific predictions which I attempted to test in my thesis:

1. I expected that the most isolated male territories would have a lower pairing success.
2. I expected that in the most isolated patches there would be a lower proportion of males with females.
3. I expected that more females would find the larger patches more easily and therefore these patches would have a higher pairing success.

I also wanted to test if there could be a difference in habitat quality and if this could influence on female choice of a mate. I also wanted to see if the number of males in a patch could influence on the number of females in the patch. More males singing in a patch could result in more females attracted, but more males mean more competition for a mate. Whether a larger number of males in a patch benefits the males, depends on the per capita rate of female attraction; males benefit when the number of females attracted increases more than the number of males present.

2 METHODS

2.1 Study species

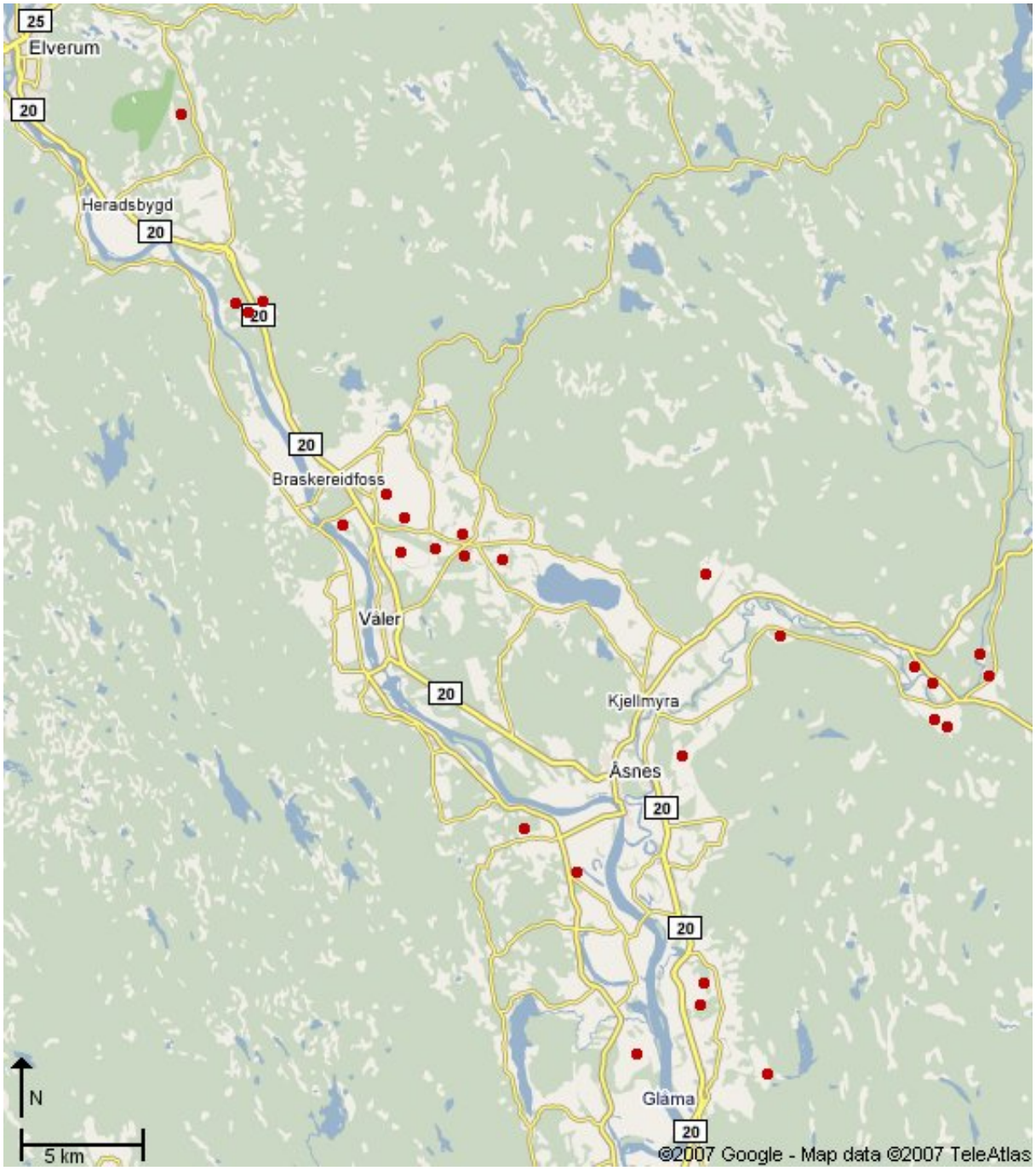
The ortolan bunting (*Emberiza hortulana*) has suffered a massive decline in most of Europe, local extinctions and within most of its distribution range it is found in many isolated populations (Kutzenberger 1994). In Norway it was a common bird in farmland areas until 1950s, but the population has since declined dramatically (Haftorn 1971, Gaarder 1995, Dale & Hagen 1997).

The ortolan bunting is a small, migratory passerine bird, which winters in tropical Africa (Cramp & Perrins 1994). After arrival to the breeding areas, males establish a territory not far from farmland (Dale 2000, Dale & Olsen 2002) and start singing to attract a female. Males arrive from the beginning of May whereas females arrive about one week later (Stolt & Fransson 1995). The female pairing period usually lasts until the beginning of June, depending upon weather condition and arrival time at nesting grounds. The female does nest building and the nest is placed on the ground, usually hidden in the ground vegetation. The female incubates the eggs alone while the male stays on guard. The (2) 3-5 eggs (Steifetten 2006) hatch after 11-12 (13) days and the nestlings stay in the nest for about 12-13 days, usually leaving nest before able to fly. The species is monogamous.

2.2 Study area

This study took place during the breeding season of 1999 in the southeastern part of Norway. The whole Norwegian ortolan bunting population occurs here, divided into a number of patches. The 500 km^2 study area (see map, Figure 1a and 1b) covered the distribution area for 90 % of the population, which is found in the central parts of Hedmark County, while the remaining 10 % found in Akershus County was not included in this study. In 1999 a total of 187 males were found in 27 patches throughout the whole area, with a range of 1-26 males in each patch.

The study area is rather flat and has an inland climate with rather poor soil conditions that makes the area dry and forest regrowth slow, for instance after forest clear-cuts and forest fire. These conditions make the area most suitable for pine forest, which is the dominant tree species. Most of the patches with ortolan buntings were found on peat bogs, forest clear-cuts, recently cleared ground and on forest burn (see below) close to mixed farmland.



Map *The map shows how the local population patches (red dots) with ortolan buntings were spread out over a 500 km^2 area.*

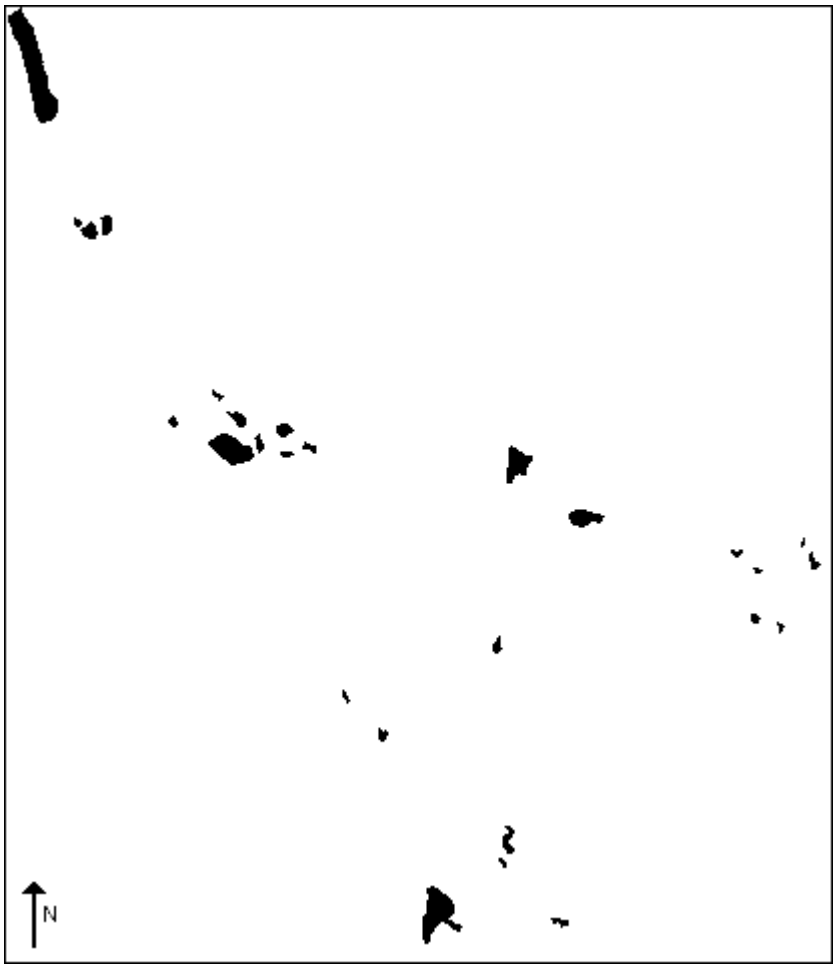


Figure 1 *The figure shows all local population patches with their relative size to each other.*

2.3 Fieldwork

Most patches were known prior to the present study (Dale & Hagen 1997). Additional patches were located by visiting suitable habitat in the study area. All known patches were searched with 1-3 days interval throughout the whole breeding season by slowly walking through the terrain in such a way that all singing males should be detected. Males were carefully recorded on to a map together with details on their behavior. Each male territory was given a coordinate using a GPS, Garmin 12. This was measured from the expected center of each territory, which was based on observations from the whole breeding season. Each territory coordinate was logged into the GPS.

It was crucial to catch and colour ring as many male individuals as possible, since only 25 males in the study area had colour rings from earlier investigations. This was most efficiently done before or around sunset with mist nets and playback. Each captured male was given a unique combination of three colour rings and one numbered metal ring. Thus, a total of 94

males had colour-rings (64 % of all males). Many males stayed unringed through most of the breeding season, but frequent visits to each site and detailed notes of singing males and their locations made it possible to separate most of the individual males and their territories.

Observations were made during two periods. The first from 12 May – 1 June which included the pairing period. The second from 8 – 26 June included the nestling period.

2.4 Habitat descriptions

I divided the patches into four main categories based on their dominant habitat (1) forest burn, (2) peat bogs, (3) forest clear-cuts and (4) recently cleared ground. Individual male territories were also categorized into the same four habitats, making a more small scale analyses possible. Habitat characteristics common to all the patches were scattered pine trees (*Pinus sylvestris*) of different age on poor soil often combined with young birch *(Betula pubescens)* trees. The ground vegetation differed somewhat among the four categories. Another common factor for most of the patches was the influence by man either by burning, cutting trees, harvesting peat or clearing ground, for agriculture.

Forest burn: In 1976 there was a huge forest fire in the study area leaving a big area of burned ground. Regrowth of vegetation in this area has been very slow, due to very poor sandy soil. Small pine trees were common, but the area had fewer birches than the other three habitat categories. Ground vegetation mostly consisted of lichen (*Cladonia* spp.) and scattered heather (*Calluna vulgaris*). There was only one patch in this habitat category.

Peat bogs: Natural, drained or commercially exploited peat bogs. Mostly consisting of scattered pine and birch trees. Numerous birches especially in undisturbed areas, as along drain ditches and on the driest and oldest parts of the commercially exploited driven bogs. Ground vegetation mostly consisted of dwarf birch (*Betula nana*), heather, harestail (*Eriophorum vaginatum*), cranberry (*Vaccinium oxycoccus*), northern bilberry (*V. uliginosum*), bilberry (*V. myrtillus*), bog rosemary (*Andromeda polifolia*) and mosses (*Sphagnum* spp.*)*. The three first mentioned are especially important for hiding the nest. Eleven patches fitted this habitat category.

Forest clear-cuts: Areas where the tall and dense pine forest had been cut which made the area open, only with some scattered tall pine trees. The older the clear-cut, the more regrowth of pines and birches. Ground vegetation was most often dominated by grasses or heather and lichen (*Cladonia* spp.), but also clusters of raspberries (*Rubus idaeus*) and herbs like rosebay willow herb (*Epilobium angustifolium*) were typical. On the individual level there were cases where males had territory on a clear-cut on a peat bog. In most of these cases it was obvious that the habitat had not been suitable if the forest had not been cut and therefore these territories were categorized as clear-cuts. Eight patches fitted this habitat category.

Recently cleared ground: This habitat category usually had rather small habitat patches which seemed quite unsuitable or marginal as a territory. Habitats placed within this category were small local sand-pits with marginal adjacent patches of vegetation, gardens with lawns, some bushes and a few trees, recently cleared farm ground with long piles of roots still laying on the ground overgrown by small bushes of birch, raspberries and herbs, very small dense islands of birch in the middle of farmland without any suitable vegetation on the ground for hiding a nest and a row of birch trees with hardly any ground vegetation around them except a little bit of grass. Four patches fitted this habitat category.

All patches were classified after main habitat to one of the categories above, but within a patch, territories could be classified as belonging to one of the other habitat categories. Three patches had equal amount of territories belonging to two different habitat categories and these patches could therefore not be assigned to any dominant habitat.

2.5 Isolation measures

Isolation measures were calculated to find if a male's isolation in relation to other males could influence on pairing success. I calculated two measures of isolation on the territory level. In the same way I calculated two measures of isolation on patch level in relation to where other patches were situated. Based on the male territory GPS coordinates I could calculate distances between all territories in the whole study area.

Two measures of isolation on the territory level were calculated based upon the GPS coordinates. First, a male's isolation in relation to other male's isolation on a small scale (usually within the same patch) was estimated as the average distance to the two closest

males. Second, a male's isolation in relation to other males isolation at a larger scale (often among different patches), estimated as the average distance to the nine closest males. The reason for choosing two isolation measures is that they will show different patterns. A frequency diagram which showed the distribution of males in each patch was used as a tool to define the two isolation measures on the territory level (see Figure 2).

Two measures of isolation were also estimated on the patch level. The distance between two patches was defined to be the shortest distance between two males belonging to separate patches. First, a patch's isolation in relation to the closest other patch was estimated. Second, a patch's isolation in relation to the three closest patches was estimated. In the study area some of the patches were more or less clustered. To be able to analyze isolation on patch level in two different ways I chose the distance to the nearest patch because it often was within the cluster of nearby patches and the average distance to the three nearest patches because it could be outside the cluster of patches. In this way the most isolated patches should stand out.

2.6 Patch delimitation and patch size

Each patch was defined according to a set of criteria. (1) The forest burn, peat bogs, newly cleared ground or clear-cuts were defined as a patch following the natural edges of this habitat. (2) If the distance between two patches were short enough for me to be able to hear males belonging to the different patches singing, the two were lumped together. This was only necessary in one case. (3) In a few cases the definition of a patch included both a clearly defined patch and a few single males sitting close by (but outside audible singing range of the other males) on different habitat patches like newly cleared ground. In these cases the area of the small habitat patches were calculated separately and included with the main patch. All patch sizes were measured with a Planix 5000 (an area/distance estimator from Gundersen & Løken), which calculated the area in km^2.

2.7 Definition of male status

Pairing status and breeding success were recorded as far as possible. Males were defined as paired if (1) a nest was found in the territory, (2) the male was seen with food in the bill during the nestling period, (3) the male was heard alarm calling for prolonged periods of time during the nestling period, or (4) the male was seen together with a female at some time during the breeding season and also had very low song rates during the main pair formation

period (end of May and beginning of June) (Dale & Hagen 1997). Male ortolan buntings usually sing less from time of pairing until egg laying is completed than before and after this period (S. Dale personal observation). Males were defined as unpaired if they were never seen associated with a female or sang frequently throughout the period they were present in the study area. Fourty males that had an uncertain pairing status or stayed less than three days in the study area were excluded from the analyses.

2.8 Statistical analyses

All statistical analyses were made using JMP 4.0.2 (Academic) 1989 - 2000 from SAS Institute Inc. Most statistical tests are non-parametric and all are two-tailed. For the ANOVA-test the data were arcsin and log transformed to obtain normality.

3 RESULTS

3.1 General patterns

Pairing success

In total I recorded 187 males in the study area, 40 males had to be excluded from further analyses because their status were uncertain. Of the 147 males, 91 (62 %) attracted a female while 56 (38 %) did not. Between the 27 patches the pairing success varied from 0 % to 100 %, with the average being 70 %.

I checked if there was any difference in pairing success in relation to day of arrival among males, but no difference was found (χ^2=2.17, df=1, p=0.14). Therefore, day of arrival will be left out from the further analyses.

Male territories and patches

Looking at the frequency distribution of the number of male territories in the patches, about half of them held less than three males (n=14) and more than half of the patches held less than nine males (n=22), (see Figure 2). This was used as a tool to choose the two different isolation measures on the territory level, which were the distance to the two and to the nine nearest males (see methods).

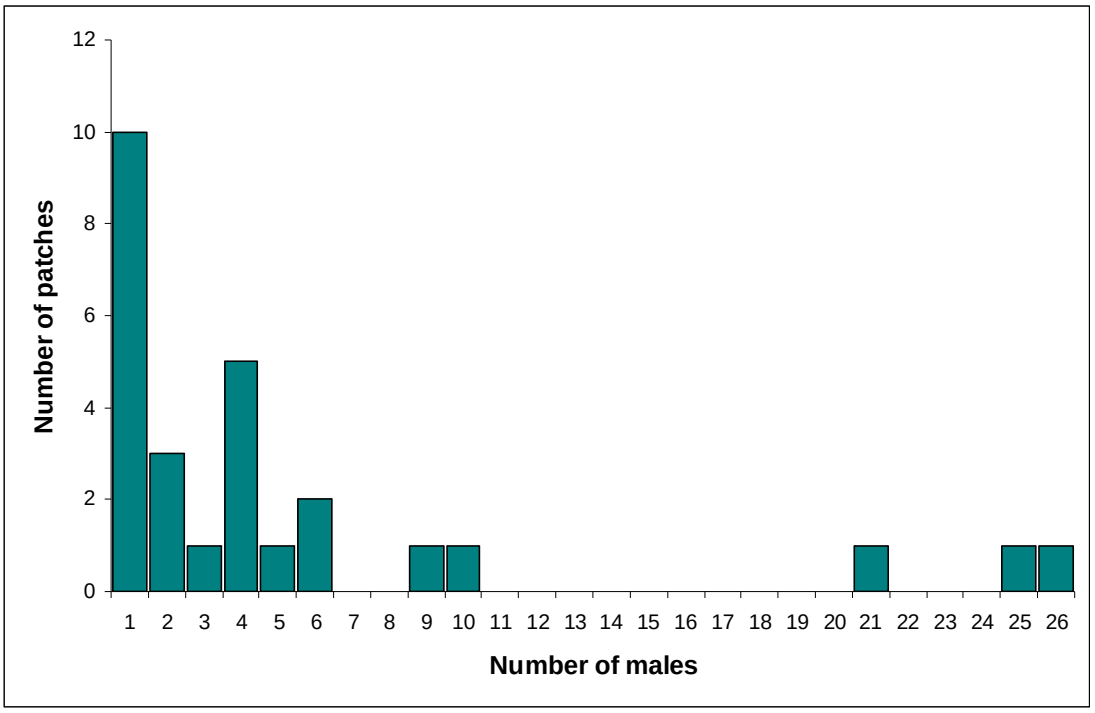


Figure 2 *Number of males in the 27 patches included in the study.*

I suspected that there was a correlation between patch size and patch population size which also was confirmed by a Spearman rank correlation (r_s=0.68, n=27, p=0.0001, see Figure 3). Even though a significant correlation was found I considered it valuable to use both factors in the further analyses to see if any of them could have an effect on pairing success.

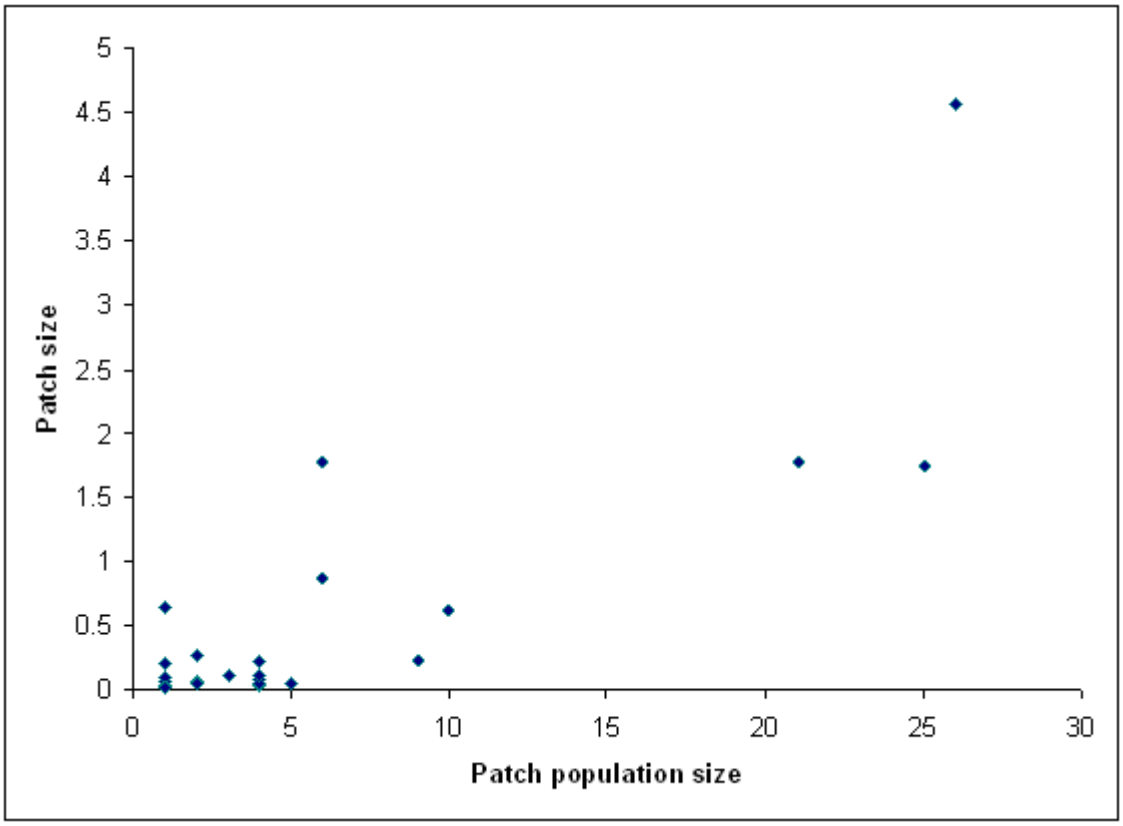


Figure 3 *Correlation between patch size and patch population size.*

Habitat

Most of the territories were on peat bogs and all in all 48 % were found in this habitat. Among the other types of habitat which was forest burn, clear-cuts and recently cleared ground the territories were divided at 18 %, 16 % and 18 % respectively.

Of the 24 patches (3 patches were excluded because they had no dominant habitat) the most common habitat were peat bogs which was found in 46 % of the patches. Forest burn, clear-cuts, and recently cleared ground were found in 4 %, 33 % and 17 % of the patches respectively.

In some of the analyses on patch level, patches lacking a dominant habitat had to be excluded together with the only patch of forest burn.

3.2 Effect of isolation

Analysis on territory level

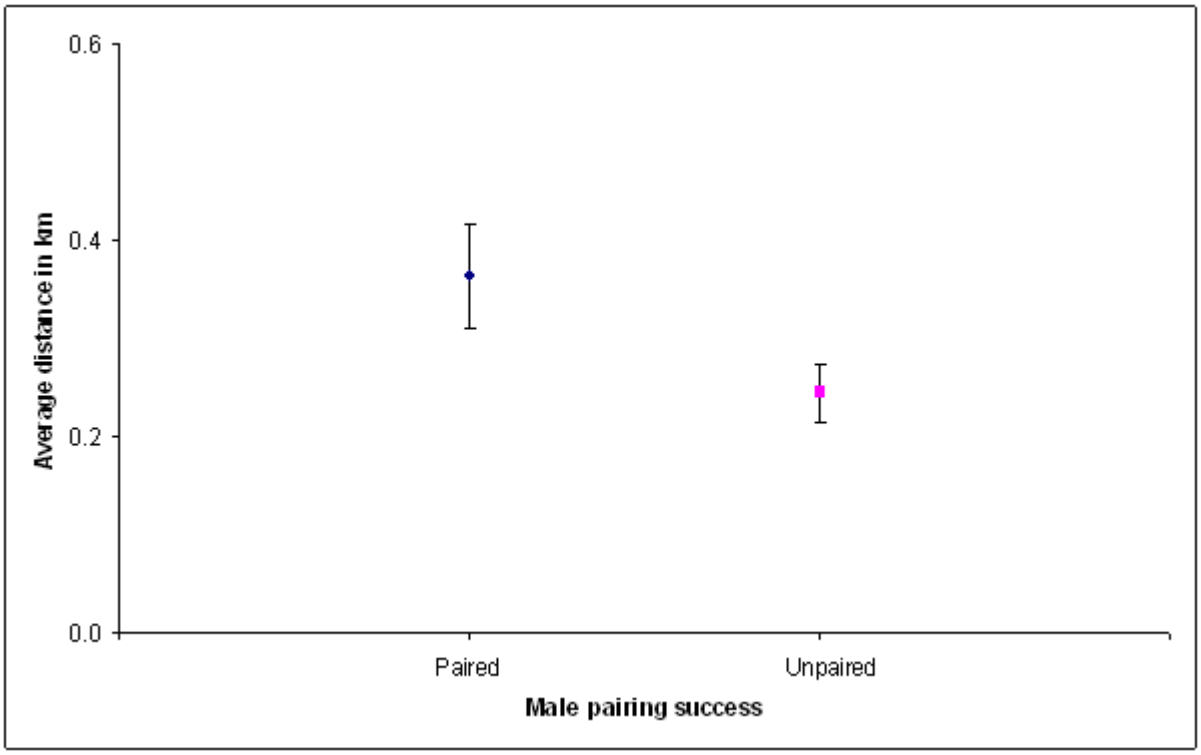


Figure 4 *Male pairing success in relation to isolation measure to two nearest males.*

Regardless of pairing success the average distance to the two nearest males had a range of 0.06-3.55 km and overall average was 0.32 km. Considering male pairing success the average distance between a male that attracted a female to the two nearest males were 0.36 km, while for the males that didn't the distance were 0.24 km. Logistic regression was used to detect a possible relationship of the effect of isolation on pairing success. An almost significant relationship was found, (χ^2=3.47, df=1, p=0.063, see Figure 4).

The second isolation measure showed that regardless of pairing success the average distance to the nine nearest males had a range of 0.21-6.00 km and overall average was 1.11 km. Considering male pairing success the average male distance to the nine nearest males were 1.13 km for those that attracted a female and 1.08 km for those which didn't. No significant relationship was found (χ^2=0.066, df=1, p=0.80, see Figure 5).

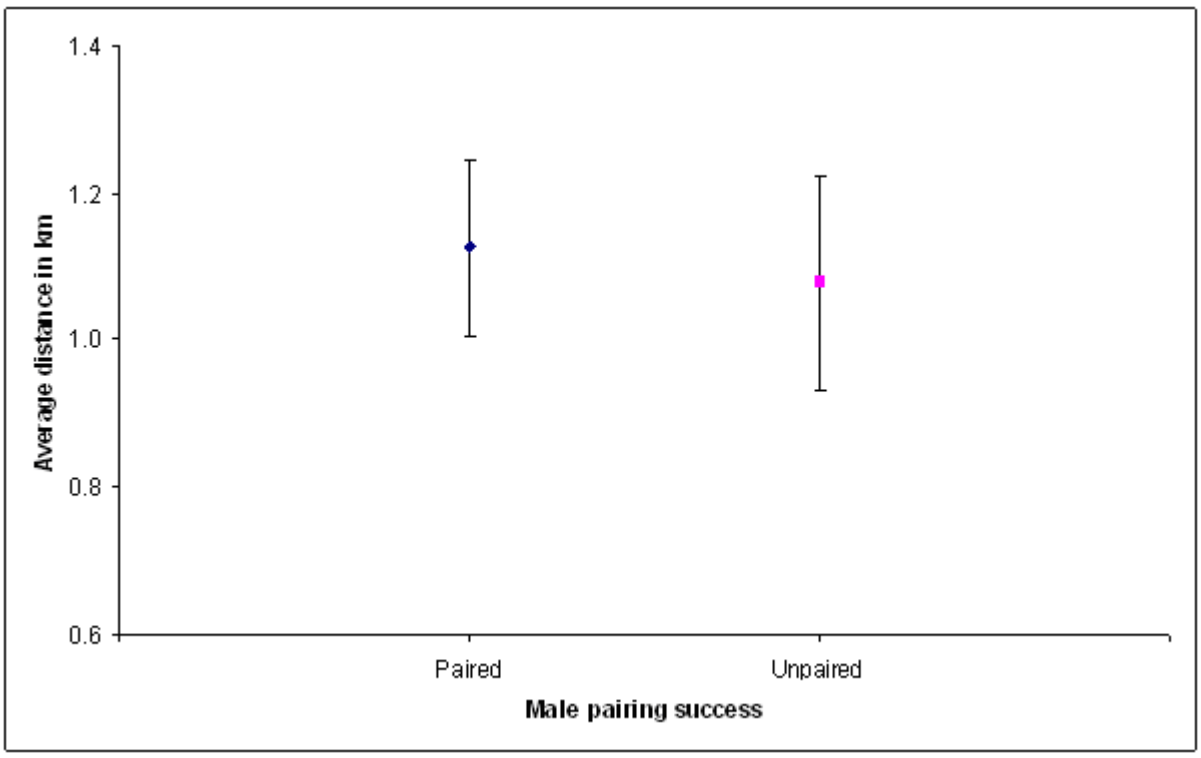


Figure 5 *Male pairing success in relation to isolation measure to nine nearest males.*

Analysis on patch level

Some of the patches were more isolated than other patches and some attracted more females than others. Female proportion among males in relation to patch isolation was analysed using two different isolation measures. Patch distance to the nearest and to the three nearest other patches were chosen. Regardless of female proportion the range between the nearest patches was 0.48-5.79 km with an overall average at 1.63 km. Between the three nearest patches the range was 0.96-6.32 km with an overall average at 2.77 km. There were no significant effects of the two patch isolation measures on the proportion of males which were paired (r_s=-0.098, n=27, p=0.63 and r_s=0.12, n=27, p=0.55 see also Figure 6 and 7).

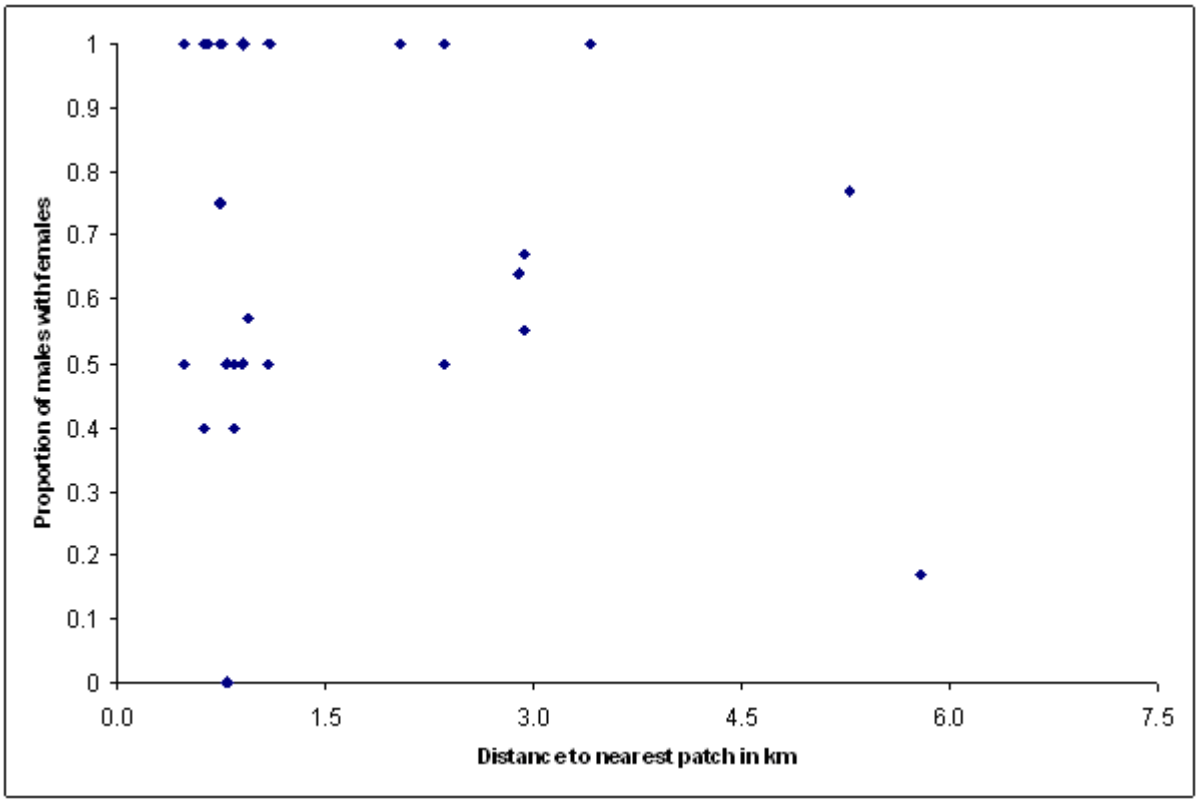


Figure 6 *Proportion with female and patch isolation to the nearest patch.*

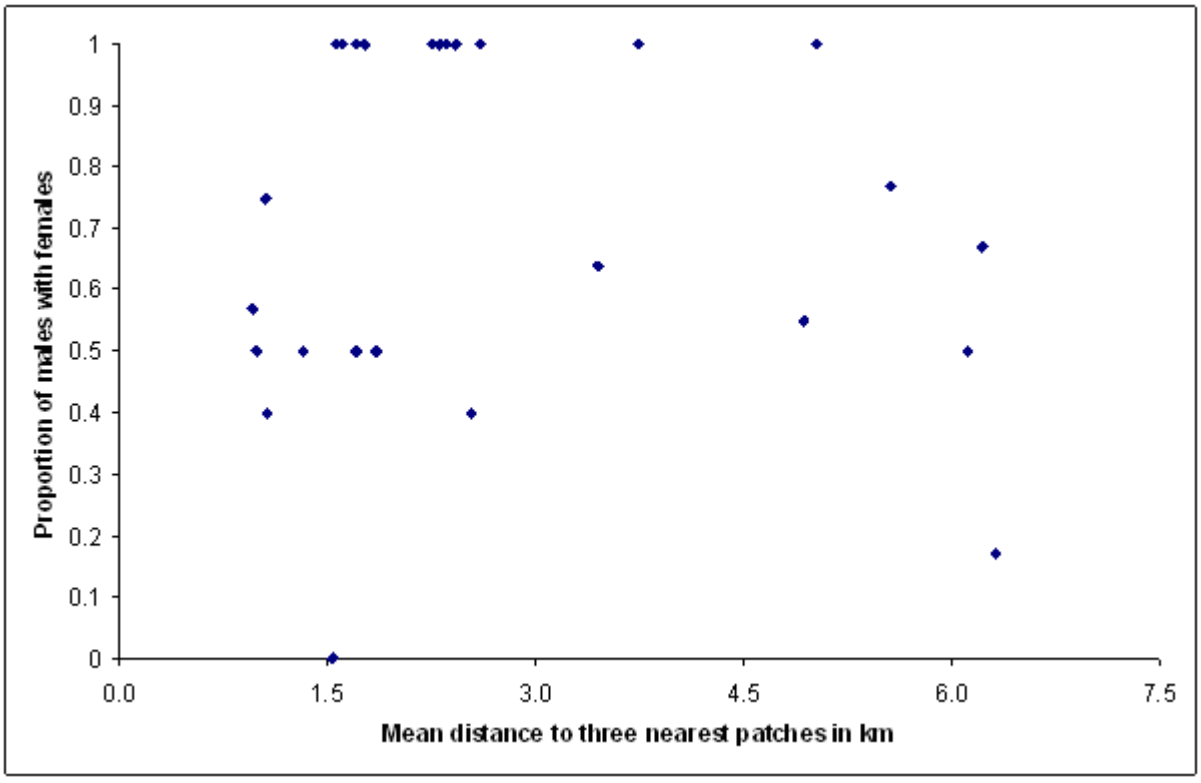


Figure 7 *Proportion with female and patch isolation to the three nearest patches.*

3.3 Effect of habitat

Analysis on territory level

Pairing success was analysed in relation to habitat in territories. Male territories were categorized into four different habitats – forest burn (26), clear-cuts (24), peat bogs (70) and recently cleared ground (27). A Contingency analysis was used to test if some of the habitats had an effect on pairing success. A highly significant relationship was found in territories were males had chosen recently cleared ground (χ^2=15.7, df=3, p=0.001, see Figure 8)

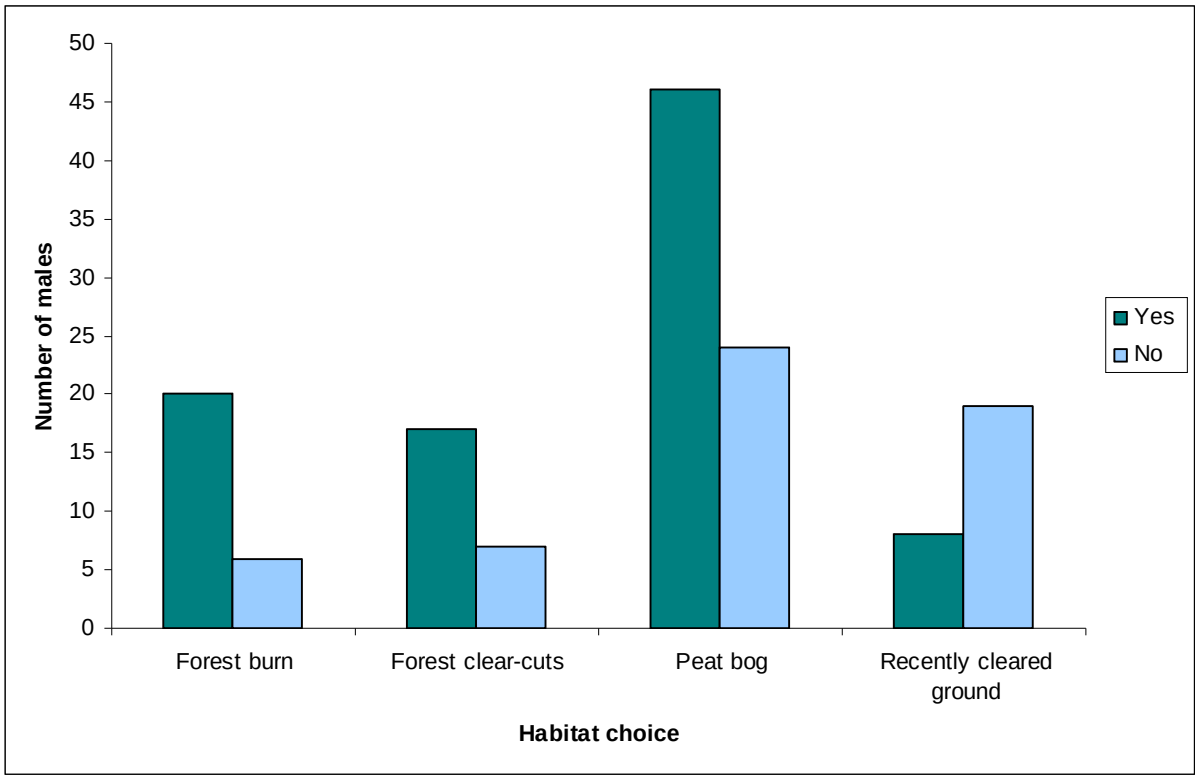


Figure 8 *Male pairing success and habitat choice.*

Analysis on patch level

Considering effect of habitat on pairing success on patch level, proportion of males with female was used to detect a possible relationship. An ANOVA-test was used but showed no significant relationship (F=0.59, df=2,20, p=0.57). In this analysis four patches had to be excluded, among them the only patch of forest burn, due to small sample size within the group. The others patches were excluded because of no dominant habitat. There were few patches of recently cleared ground, and in three out of four patches there were only one male which all succeeded in attracting a female. This fact is having a skewed affect on the result of the figure (Figure 9).

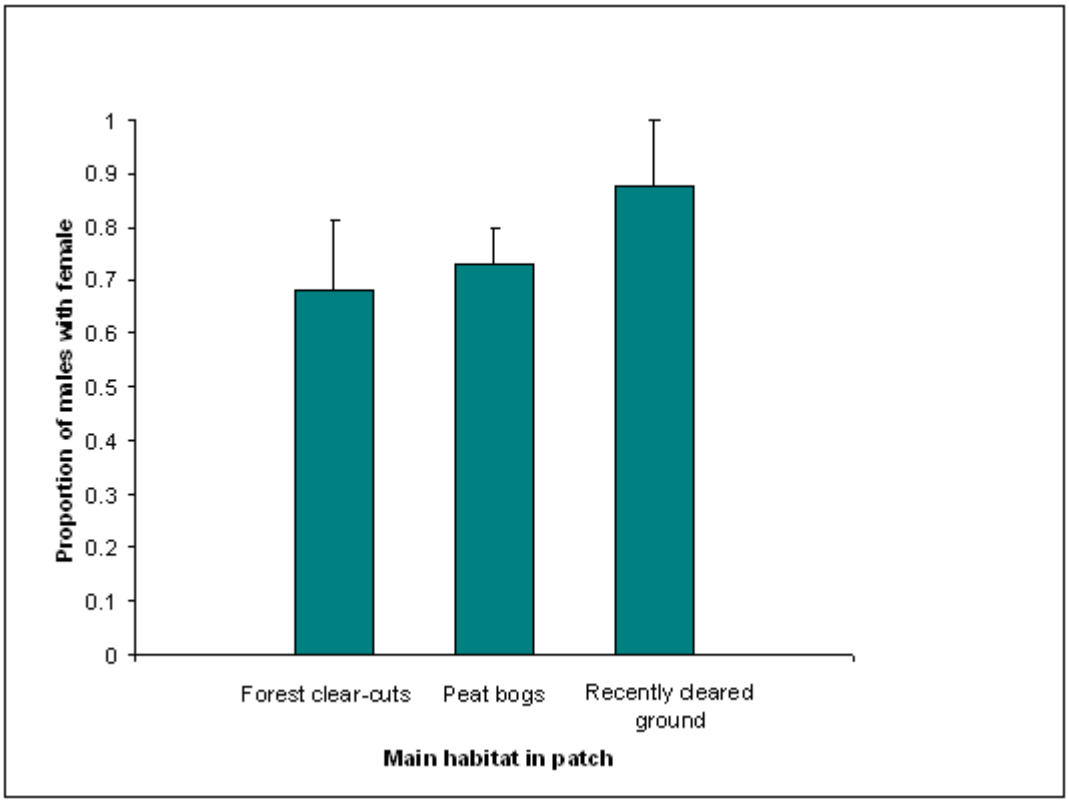


Figure 9 *Proportion of males with female in relation to main habitat in patches.*

3.4 Effect of patch size

Analysis on territory level

The patch size varied from 0,01 – 4,57 km^2, with an overall mean at 0.51 km^2. Since there was a rather distinct variation in patch size I examined if this could influence on male paring success on the individual level. Logistic regression was used to detect a possible relationship, the outcome of the test was not significant (χ^2=1.56, df=1, p=0.21, see Figure 10).

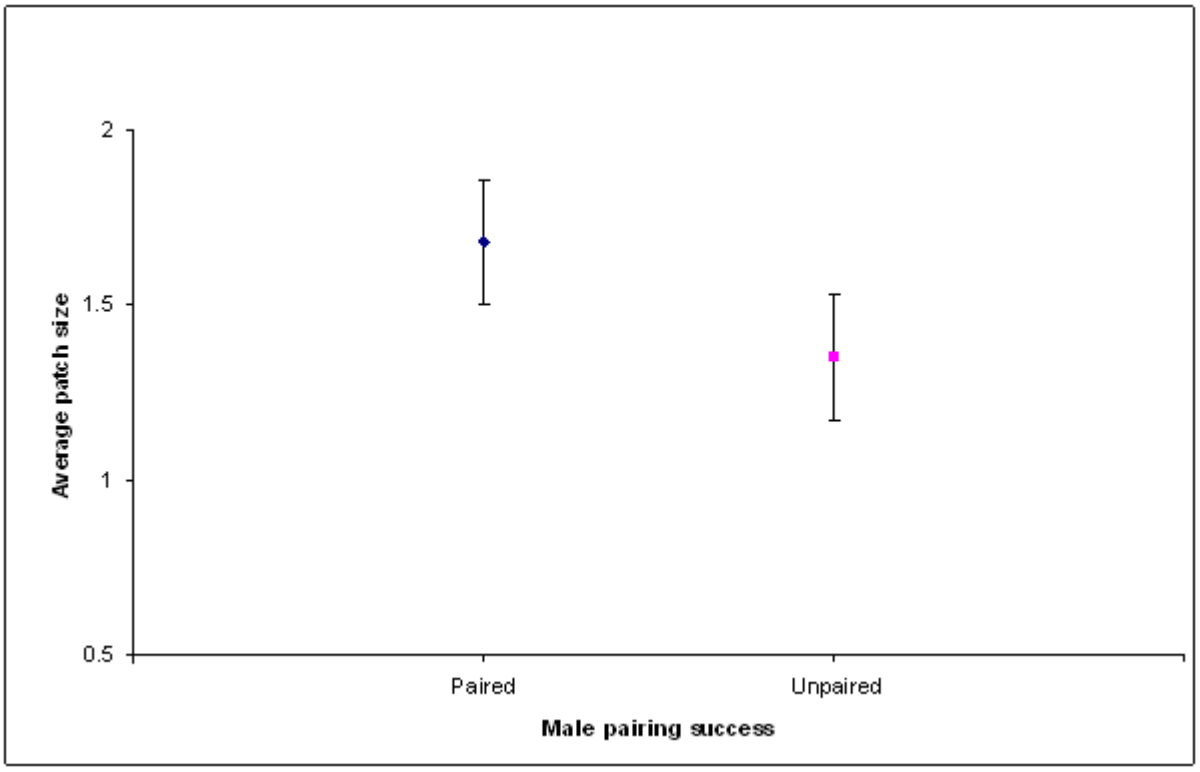


Figure 10 *Male pairing success in relation to average patch size.*

Analysis on patch level

I also examined if patch size had an effect on the pairing success among males by looking at the proportion of females in a patch. I used a Spearman rank correlation to detect possible relationships between the two factors, but the test showed no significance (r_s=-0.21, n=27, p=0.28, see Figure 11).

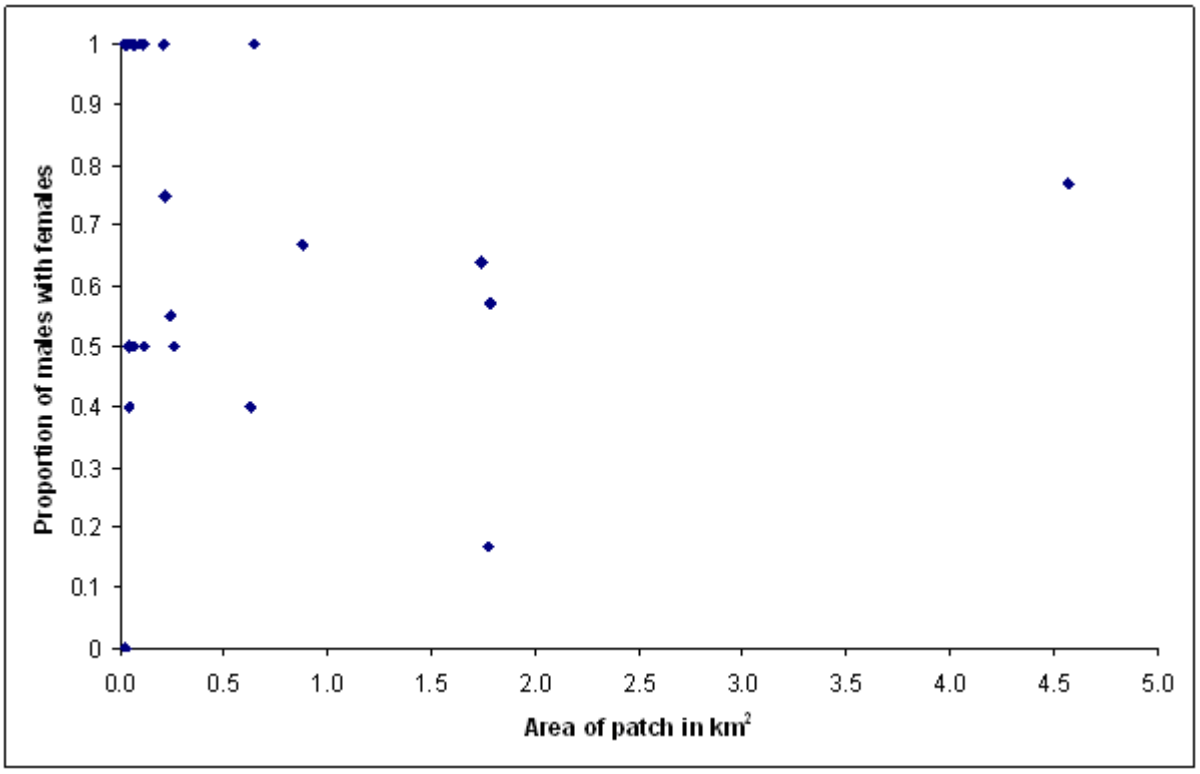


Figure 11 *Proportion of males with female in relation to patch size.*

3.5 Effect of patch population size

Analysis on territory level

The number of males in one patch varied from 1-26 individuals. Many singing males in one spot could attract more females than one male is singing in a patch. Therefore population size was tested for a possible relationship and again paring success on territory level was used as a response. No significance was found using logistic regression (χ^2=0.68, df=1, p=0.41, see Figure 12).

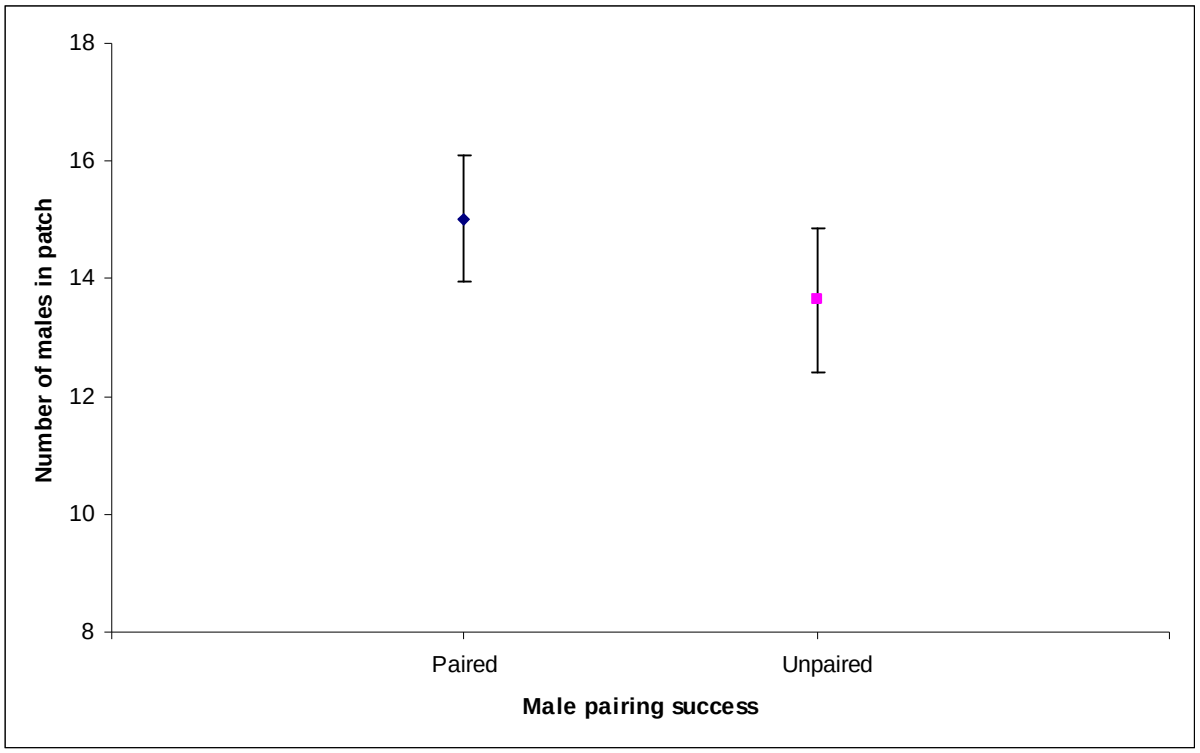


Figure 12 *Male pairing success in relation to patch population size.*

Analysis on patch level

I tested if the proportion of males attracting a female at patch level could be influenced by the number of males in the patch. A Spearman rank correlation was used and showed a significant relationship between the two factors (r_s=-0.56, n=27, p=0.002, see Figure 13).

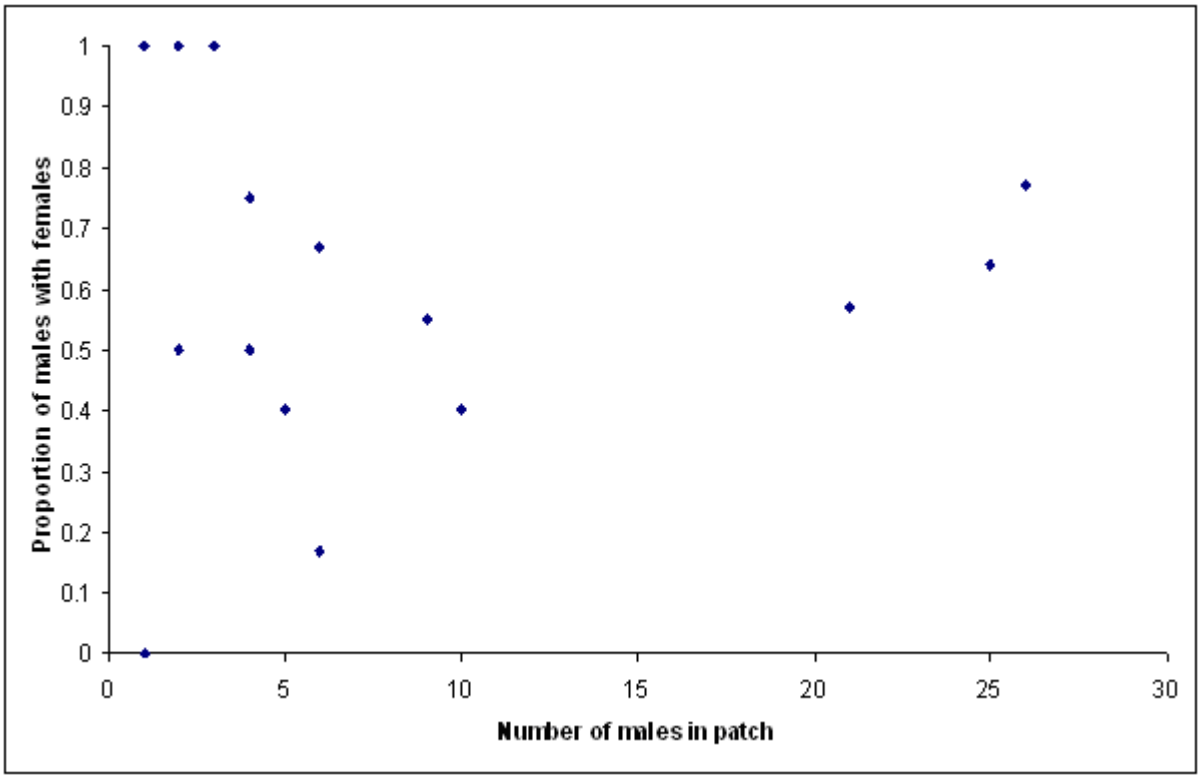


Figure 13 *Proportion of males with female in relation to patch population size.*

3.6 All factors considered in multiple analyses

Analysis on territory level

All factors were tested in a logistic regression analysis to see if any of the factors still showed any significance. Isolation to the two nearest and nine nearest males showed no significance (χ^2=2.22, df=4, p=0.14 and χ^2=0.17, df=4, p=0.68). Choice of habitat seemed to have a highly significant effect on pairing success (χ^2=16.5, df=4, p=0.0009). Patch size and patch population size turned out not significant (χ^2=3.27, df=4, p=0.071 and χ^2=1.92, df=4, p=0.17).

Analysis on patch level

All factors were also tested in an ANOVA-test after transformation of data for normality and after patches had been categorized by dominant habitat. The patch of forest burn and all patches of recently cleared ground had to be excluded because of small sample size. No significance were found within the habitat peat bog (F=1.02, df=4,6, p=0.47) and clear-cuts (F=0.86, df=4,3, p=0.57).

4 DISCUSSION

This study has tried to find support for the hypothesis presented by Dale (2001b), that pairing success within small and fragmented populations may also be affected by degree of isolation. Pairing success was low in the study area and only 62 % of the males attracted a female. Female-biased natal dispersal has been suggested as an explanation for the large number of unpaired males and that females have difficulties in locating males because the patches are distributed over large areas (Dale 2001b, see map and Figure 1). Mate location should also be easier in larger than in small patches and patch isolation degree should also influence negatively on mate location and thereby pairing success. My results did not confirm that isolation have any negative effects on male pairing success within the study area of the population, neither on a territorial level or on patch level, and therefore none of my first two predictions could be confirmed. Studies from the same area in later years have found the same result, even though a considerable amount of data from several years was included (Steifetten 2006). Even though Dale (2001b) found indirect evidence that such an effect operate between populations, it could still be found within a population, all though it must be on a bigger scale than in this study.

Looking at the decline of the ortolan bunting population in Norway there have been an obvious tendency that males seem to vanish from the outermost periphery of the population. This may suggest that there is an effect of isolation on pairing success within the population, but on a larger scale than within the 500 km^2 study area. Not many years ago birds could still be heard singing in the neighboring counties of Oppland and Akershus. In 1985 there were still 60 males found in Oppland, but in 1997 only four remained (Gaarder 1986, Dale 1997). In Akershus there were still 30 males found in 1989, but the number have steadily declined and in 2004 only two unpaired males were found (Dale 2007). The populations in both Oppland and Akershus counties may be to far from the focal population in Hedmark. The female-biased natal dispersal and male fidelity to site when older have left males unpaired and recruitment low; males have probably become more isolated through the years.

In later years the focal population has been followed closely. Males and some females have been have been color-ringed and dispersal distances have been recorded for several years. Males are capable of moving extraordinary long distances of up to 45 km. None of the males have been found to move all the way between the focal population in Hedmark and the isolated patches in Akershus (Dales personal comment). The distance between the focal

population in Hedmark and the patches in Akershus is approximately 70 km, which exceed the longest dispersal known among males of ortolan bunting. The little population in county Akershus persisted until recently but is now extinct. The small remains of ortolan buntings in Oppland and Akershus have probably been too isolated from the focal population in Hedmark and over time they became extinct.

Since isolation within the population does not seem to have an effect on pairing success the chance of attracting a female should be the same throughout the whole study area. Males may use other cues to increase fitness. Dale (2001b) proposed in his sex-biased dispersal hypothesis, among other predictions, that the vulnerability to decline and extinctions should be higher in small habitat fragments. Patch size could influence on pairing success and one should expect that there would be a larger chance for a female to visit a bigger than a smaller patch (Dale 2001b). Studies have shown reproduction differences between small and large forest fragments (Porneluzi & Faaborg 1999, Kuehl & Clark 2002), but the reason for these differences could be other than sheer female attraction (i.e. parasite exposure and predation). I expected to find that small patches followed such a pattern, but my results showed no difference in pairing success in large and small patches within the population and therefore my third prediction could not be confirmed.

Since either isolation or patch size seem to influence on pairing success within the population it could seem to support Dales hypothesis that the females disperse in an evenly manner throughout the terrain (Dale 2001b). But it has been showed that males within the study area can undertake major breeding dispersal distances in great excess and in such a short time (within days) that a male could easily disperse in every direction throughout the whole study area (Dale et. al. 2005). Steifetten (2006) tried to find reasons for this behaviour and found that males dispersed from patches low in females to patches with more females. But no increase in pairing success was found among the males that undertook these breeding dispersals. In my study I had several cases were patches only inhabited one paired male and which was not accompanied by other males. This gives some support to the hypothesis that females spread out more evenly in the terrain and encounter a male randomly, rather than the hypothesis that male breeding dispersal should influence on pairing success.

Females may choose patch by other cues, for instance could the number of singing males in a patch influence on female attraction. More males singing in a patch could be easier to locate from the air than a few. To rule out whether or not this could influence on pairing success within the population I also tested for patch population size. Preliminary result

showed some significance that the number of males in patch could have some effect, but the main result showed no significance of such an effect on pairing success within the population.

Habitat quality could influence on female choice of where to settle. Burke & Nol (1998) found that small fragments had more unpaired males than large, and a possible explanation for this was that the smaller patches had lower abundance of food and lack of nesting sites. Differences in habitat quality could lead to differences in pairing success among habitat patches. In the study area there were four main habitats – peat bogs, forest burn, forest clear-cuts and recently cleared ground - and I tested if any of them could influence on pairing success. On a territory level recently cleared ground had a highly negative effect on pairing success. In this habitat category a wide variation of habitats were included like small, local sand-pits with marginal adjacent patches of vegetation, gardens with lawns, some bushes and a few trees, recently cleared farm ground with long piles of roots still laying on the ground overgrown by small bushes of birch, raspberries and herbs, very small dense islands of birch in the middle of farmland or a row of birch trees with hardly any ground vegetation around them except a little bit of grass. This variety within this habitat category could influence on the result, but common for all the territories in this habitat category were their small size and they often seemed quite unsuitable or marginal; due to the lack of the preferred ground vegetation where the nest usually was hidden. Later studies in the area have shown that most of these marginal territories have not been used which also could be an indication that habitat quality is to poor (Dale personal comment). In territories placed on peat bogs, forest burn and forest clear-cuts there were no effect of habitat quality on pairing success, and there was not a large difference in pairing success between them. An explanation for low pairing success in the territories with recently cleared ground could be that these territories are more isolated than territories of other types of habitat. But when testing for isolation together with habitat in main results I found no relation between the two factors.

On a patch level the effect of habitat quality was not found, but with a larger sample it could also turn out to have some influence on pairing success.

4.1 Implications for conservation biology on population viability

Other factors than isolation within the population must be more important for the viability of the population of ortolan buntings. But the fact that 38 % of the males were unpaired is still a strong indication that the population is heading towards extinction and that it is a highly endangered species.

My study confirm Dales (2001b) assumptions that female disperse evenly out into the terrain, because even in small and isolated patches males could have pairing success without being accompanied by other unpaired males. This means that even small patches within the population could be valuable for the viability of the species. In management plans it should therefore be of utmost importance to preserve all patches were the species occur. Also suitable patches in the remaining distribution range of the population should probably also be set aside and managed in a way that makes it suitable for the ortolan buntings for years to come.

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